

Spores of *Lycopodium* and *Selaginella* of North Pacific America

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Received May 18, 1987

HEUSSER, C. J., and PETEET, D. M. 1988. Spores of *Lycopodium* and *Selaginella* of North Pacific America. *Can. J. Bot.* **66**: 508–525.

Morphological descriptions and keys apply to spores of eight species of *Lycopodium* (*L. alpinum*, *L. annotinum*, *L. clavatum*, *L. complanatum*, *L. inundatum*, *L. obscurum*, *L. selago*, and *L. sitchensis*) and seven species of *Selaginella* (*S. densa*, *S. douglasii*, *S. oregana*, *S. selaginoides*, *S. sibirica*, *S. wallacei*, and *S. watsonii*). Spores are radiosymmetric, heteropolar, tetrahedral, and trilete. The most workable characters of use in identification of spores of *Lycopodium* are type sculpture (mostly reticulate but also foveolate and rugulate) and the presence, continuity, and absence of sculpture on proximal and distal faces. Spores of *Selaginella* are distinguished by the presence or absence of a perine, perine thickness, microsculpture, and appearance of cristae. Modern, Holocene, and Pleistocene distribution records of *L. selago* and *S. selaginoides* are reviewed for the purpose of developing the Quaternary history of *Lycopodium* and *Selaginella* in North Pacific America. They illustrate the importance of refugia in Washington, the Queen Charlotte Islands, and Japan – eastern Asia, which were noteworthy distribution centers during and following Wisconsin glaciation.

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Les descriptions morphologiques et les clefs du présent article concernent les spores de huit espèces de *Lycopodium* (*L. alpinum*, *L. annotinum*, *L. clavatum*, *L. complanatum*, *L. inundatum*, *L. obscurum*, *L. selago* et *L. sitchensis*) et sept espèces de *Selaginella* (*S. densa*, *S. douglasii*, *S. oregana*, *S. selaginoides*, *S. sibirica*, *S. wallacei* et *S. watsonii*). Les spores sont de symétrie radiale, hétéropolaire, tétraédriques et trilètes. Les caractères les plus pratiques pour l'identification des spores de *Lycopodium* sont le type de sculpture (surtout réticulée mais aussi foveolée et rugulée) et la présence, la continuité, ou l'absence d'éléments de sculpture sur les faces proximales et distales. Les spores de *Selaginella* se distinguent par la présence ou l'absence d'une périne, l'épaisseur de la périne, la micro-sculpture et l'apparence des crêtes. Dans le but d'élucider l'histoire quaternaire des *Lycopodium* et *Selaginella* en Amérique du Pacifique Nord, les mentions de la distribution actuelle et de celles à l'Holocène et au Pléistocène des *L. selago* et *S. selaginoides* sont réexaminées. Les mentions soulignent l'importance des refuges à Washington, aux îles de la Reine Charlotte et au Japon – Asie orientale, qui étaient des centres de distribution reconnus au cours et après la glaciation du Wisconsin.

[Traduit par la revue]

Introduction

Identification of fossil spores of *Lycopodium* and *Selaginella* in mire peats and lake sediments of North Pacific America is basic to tracing the Quaternary history of regional species. Morphological features of some spores render species readily identifiable, for example, *L. annotinum*, *L. inundatum*, *L. selago*, *S. douglasii*, and *S. selaginoides*; others, considered problematic by palynologists, are simply designated *L. cf. clavatum*, *L. clavatum* type, *L. cf. alpinum*, *L. sitchensis* type, *S. densa* type, *S. wallacei* type, and *S. cf. wallacei* (Mathewes 1973; Mathewes and Clague 1982; Petersen *et al.* 1983; Heusser 1983a, 1983b; Heusser and Heusser 1981; Peteet 1986; Warner 1984; Warner *et al.* 1984). Recognition of certain species in the fossil record, exemplified by *Lycopodium selago* and *Selaginella selaginoides*, provides data for establishing distribution patterns and paleoenvironments since mid-Wisconsin glaciation.

The objective of this paper is to construct a morphological basis for distinguishing spores of northwest species, thus providing background needed for a regional account of the Quaternary phytogeographical relations of *Lycopodium* and *Selaginella*. The region covered is the Pacific slope from northern California to western Alaska.

Materials and methods

Previous works have described spores of *Lycopodium* and *Selaginella*, including many of the species represented here, although relatively few treatments have adopted modern descriptive terminology (*sensu* Faegri and Iversen 1975). We have drawn freely from these sources with particular reference made to Wilson (1934), Reeve (1935), Tryon (1949), Knox (1950), Harris (1955), Erdtman (1957), Erdtman *et al.* (1961), Hellwig (1969), Erdtman and Sorsa (1971), Wilce (1972), McAndrews *et al.* (1973), and Moe (1974).

Taxonomic treatment follows Taylor (1970). Spores described are from eight species of *Lycopodium* and seven species of *Selaginella*, ranging in the Pacific Northwest (Hitchcock *et al.* 1969; Taylor 1970) and in Pacific British Columbia (Calder and Taylor 1968; Taylor and MacBryde 1977) and Alaska (Hultén 1941, 1968). No attention is given to spores of subspecific combinations; megaspores of *Selaginella* are also not included.

Material used for study is from herbaria at the New York Botanical Garden (NY), University of Washington (UW), and New York University (NYU). For each species, spores from three individual collections were studied under the light microscope and scanning electron microscope. Before light microscopy, the spores were boiled in dilute KOH solution, acetolyzed, and mounted in silicone oil (Faegri and Iversen 1975). Size measurements made under Nomarski differential interference contrast using a Zeiss photomicroscope III ($N = 50$ in all but three instances, where $N = 30$) are at $400\times$. For scanning elec-

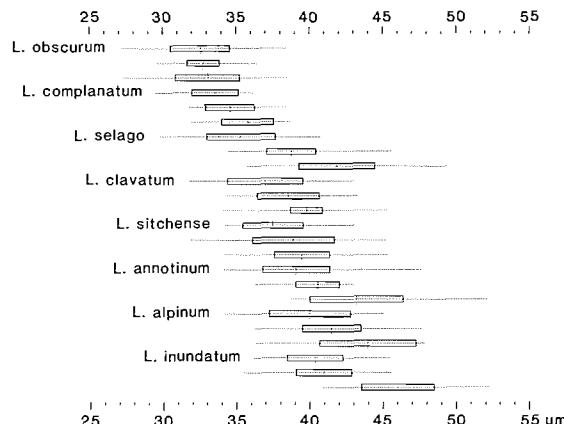


FIG. 1. Size range, mean, and standard deviation of spores of *Lycopodium* of North Pacific America.

tron microscopy, untreated spores were mounted on aluminum stubs, coated with carbon and gold-palladium in a vacuum evaporator, and examined under an AMR 1000 scanning electron microscope at either 10 or 20 kV.

Descriptions and keys

A consistent descriptive format is followed for individual spore characters: occurrence as monads or fused multiples, symmetry, polarity, shape, tetrad scars, exine thickness and sculpture, size (range, mean, and standard deviation of equatorial axes and range of the polar axis), and geographical distribution within the American North Pacific region.

Populations studied reveal certain morphological characters to be species specific, whereas other features are reliable within limits or are unreliable. As a result, strengths and weaknesses of the keys depend upon the consistency of selected spore characters. All spores occur as monads (*Selaginella selaginoides* with occasional tetrads is the only exception) and are radiosymmetric, heteropolar, tetrahedral, and trilete. Overlap in size ranges in both *Lycopodium* and *Selaginella* (Figs. 1, 2) is so great as to preclude use of size as a distinguishing character. Spores of species within each genus, in alphabetical order to facilitate location, are illustrated by scanning electron micrographs (Figs. 3-32) and light micrographs (Figs. 33-62).

For *Lycopodium*, identification to species in the key is, for the most part, defensible. Reliance is placed primarily on type of sculpture, which is mostly reticulate but also foveolate and rugulate, and on the presence, extent, and absence of sculpture covering proximal and distal faces of reticulate spores. The weakest area is with respect to the use of reticulate sculpture, especially in the identity of *L. alpinum*, *L. complanatum*, and *L. sitchense*. Distinguishing these species can be problematic because of difficulty in assessing poorly expressed sculpture in some specimens. The three are closely allied, comprising the subgenus *Complanatostachys*, containing $2N = 46$ chromosomes, and show much similar gross morphology (Hitchcock *et al.* 1969). *Lycopodium alpinum* and *L. sitchense*, for example, are not easily separated in the field. Identity of spores which are not referable to species but otherwise fall in the subgenus can be designated *L. complanatum* type.

Some authors (Hultén 1968; Hitchcock *et al.* 1969; Taylor 1970) traditionally classify regional species of Lycopodiaceae in a single genus, *Lycopodium*, whereas others (Beitel 1979) recognize multiple genera from differences in chromosome

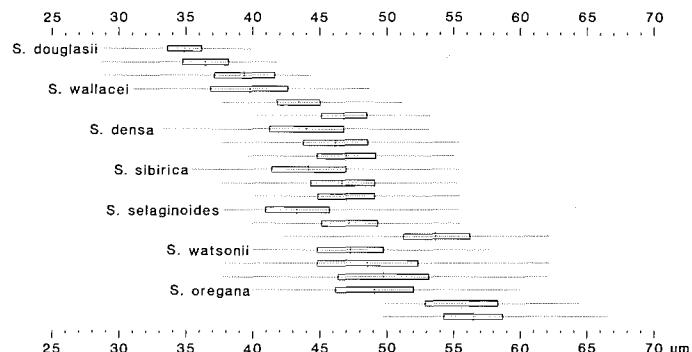


FIG. 2. Size range, mean, and standard deviation of spores of *Selaginella* of North Pacific America.

number and from diverse sporophyte, gametophyte, and spore morphology. Sculptural characteristics of spores from North Pacific American material examined here offer justification for the view of diverse genera, as followed by Taylor and MacBryde (1977) for British Columbia: *Huperzia* Bernhardi (*H. selago* (L.) Bernhardi ex Schrank & Martius = *Lycopodium selago*), *Lycopodiella* Holub (*L. inundata* (L.) Holub = *Lycopodium inundatum*), and *Lycopodium* L. (*sensu stricto*, *L. alpinum*, *L. annotinum*, *L. clavatum*, *L. complanatum*, *L. obscurum*, *L. sitchense*). For our species, sculpture in *Huperzia* is foveolate, in *Lycopodiella* rugulate, and in *Lycopodium* reticulate.

The key for *Selaginella* makes use of sculpture in conjunction with the presence or absence of a perine. Identity of spores containing a perine envelope is to a large extent dependent on perine thickness, and some reservation is expressed in the use of this character. Although workable with specimens studied, perine thickness is a tenuous feature because it often changes in the fossil state as a function of the age and character of the preserving medium. Least reliable is the distinction of *S. sibirica* and *S. watsonii* by means of microsculpture. Ranges of these species are, however, geographically remote.

Lycopodium

Lycopodium alpinum L.

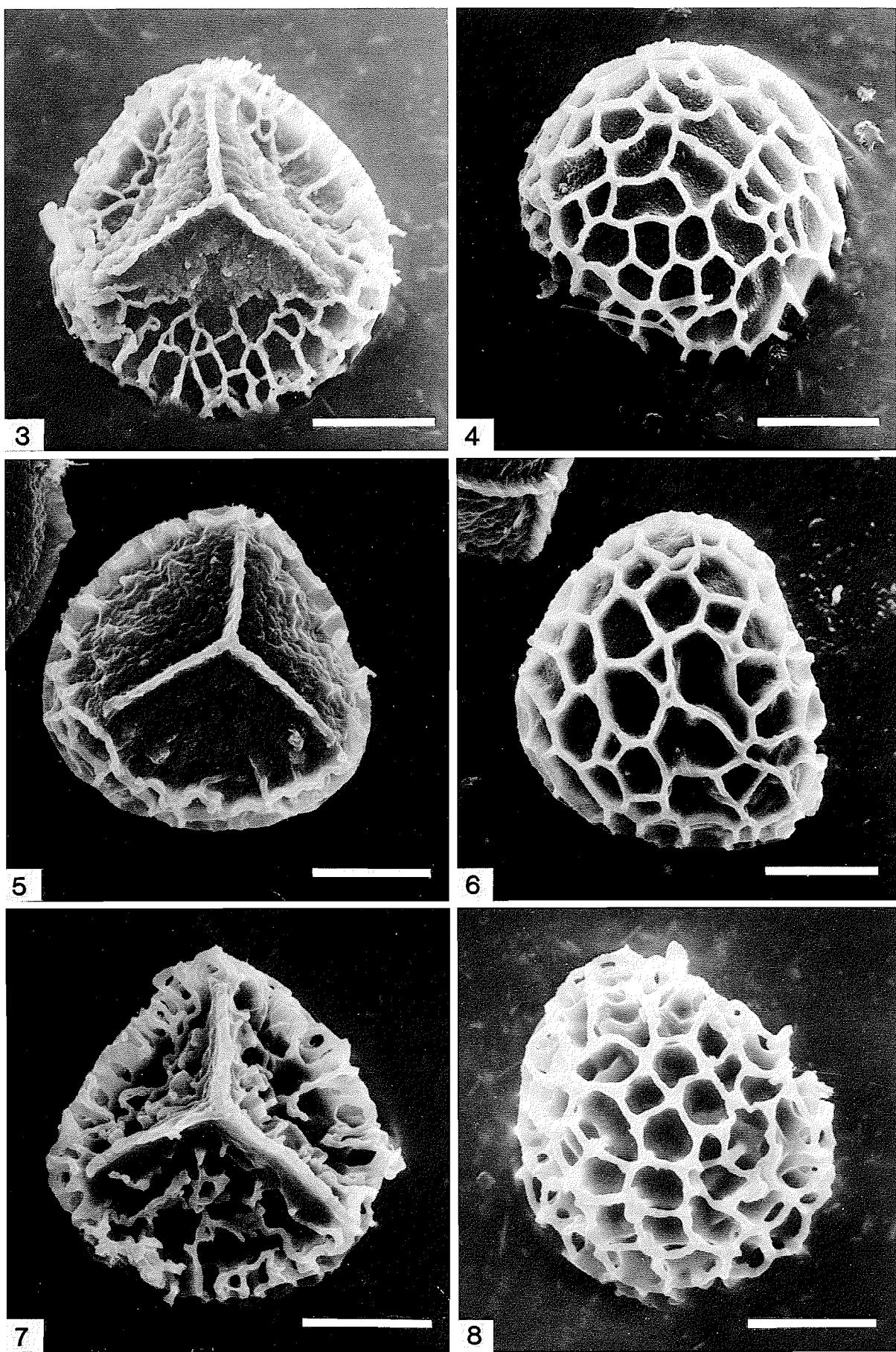
Figs. 3, 4, 33, 34

Monad, radiosymmetric, heteropolar, tetrahedral—sub-spherical; amb circular—subtriangular; trilete, laesuræ narrow, straight, 0.6–0.8 radius; exine 1 μm or less in thickness, reticulate, reticulum developed distally, extending to proximal faces but dissolving in the polar area, brochi variable, numbering 6–9 across in amb view, muri straight or somewhat curved, <1 μm thick, irregular in thickness, height ranging from 2 at the distal pole to 3 μm at the equator, lumina for the most part 6–7 μm across, elongate lumina >10–17 μm in length; 36.3–47.9 (44.0 ± 3.3) × 27.2–34.1 μm (J. A. Calder, J. A. Parmalee, and R. L. Taylor, Yanks Peak, British Columbia, 1956, UW 186168), 36.2–47.7 (41.5 ± 2.0) × 22.7–31.8 μm. (F. A. Barkley, Logan Pass, Montana, 1937, UW 41519), 34.1–45.1 (40.0 ± 2.8) × 27.0–31.7 μm (E. H. and H. B. Looff, Kodiak Island, Alaska, 1940, UW 179746). DISTRIBUTION: Aleutian Islands, Alaska, to southern British Columbia.

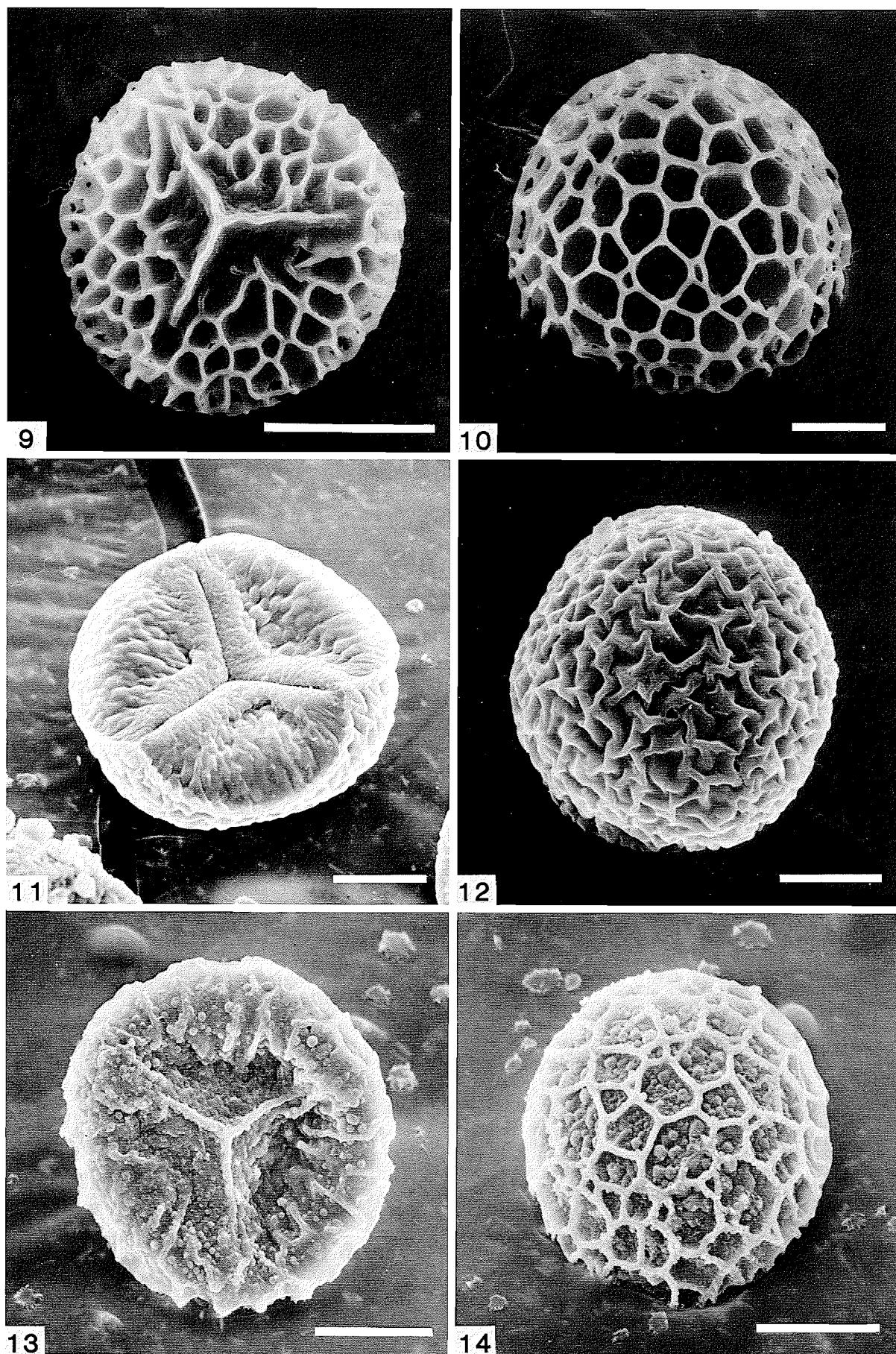
Lycopodium annotinum L.

Figs. 5, 6, 35, 36

Monad, radiosymmetric, heteropolar, tetrahedral—sub-spherical; amb circular—subtriangular; trilete, laesuræ narrow, straight, extending to the equator; exine 1–1.5 μm thick, reticulate, reticulum mostly distal; brochi variable,



Figs. 3-8. Spore scanning electron micrographs of *Lycopodium alpinum*, proximal view (Fig. 3), distal view (Fig. 4); *L. annotinum*, proximal view (Fig. 5), distal view (Fig. 6); *L. clavatum*, proximal view (Fig. 7), distal view (Fig. 8). Scale bar = 10 μm .



Figs. 9–14. Spore scanning electron micrographs of *Lycopodium complanatum*, proximal view (Fig. 9), distal view (Fig. 10); *L. inundatum*, proximal view (Fig. 11), distal view (Fig. 12); *L. obscurum*, proximal view (Fig. 13), distal view (Fig. 14). Scale bar = 10 μm .

numbering 6–8 across in amb view, muri straight or slightly curved, approaching 1 μm in thickness, thickness \pm uniform, height varying from 1 at the distal pole to 3 μm at the equator, lumina as much as 23 μm long, in places penetrated by muri branches; 34.1–47.7 (39.1 \pm 2.3) \times 25.0–29.5 μm (J. W. Thompson, Wenatchee Mountains, Washington, 1951, UW 144841), 36.3–43.1 (40.6 \pm 1.5) \times 25.2–34.1 μm (G. N. Jones, Akutan Island, Aleutian Islands, Alaska, 1936, UW), 38.6–52.2 (43.2 \pm 3.2) \times 26.0–34.4 μm (J. Hunt, Sulfur Creek, Washington, 1951, UW 191971). DISTRIBUTION: Aleutian Islands, Alaska, to northern Oregon.

Lycopodium clavatum L.

Monad, radiosymmetric, heteropolar, tetrahedral–sub-spherical; amb circular–subtriangular; trilete, laesurae straight, 0.6–0.7 radius; exine 1 μm or less thick, reticulate, reticulum developed distally, fragmented proximally, brochi variable, numbering 9–11 across in amb view, muri straight or slightly curved, <1 μm thick, irregular in thickness, height ranging from 1.5 at the distal pole to 2.0 μm at the apices and 5 μm along interapical lengths of the equatorial limb, lumina 4–6 μm across; 31.8–43.1 (37.0 \pm 2.6) \times 22.6–29.4 μm (E. H. and H. B. Looff, Kodiak Island, Alaska, 1940, UW 179747), 34.1–45.4 (39.8 \pm 1.1) \times 23.0–29.5 μm (J. B. Flett, Cleveland Peninsula, Alaska, 1901, UW 39284), 34.2–43.4 (38.6 \pm 2.1) \times 22.7–31.8 μm (J. W. Thompson, Guy Peak, Washington, 1936, UW). DISTRIBUTION: Aleutian Islands, Alaska, to northern California.

Lycopodium complanatum L.

Monad, radiosymmetric, heteropolar, tetrahedral–sub-spherical; amb circular; trilete, laesurae narrow and straight, 0.5–0.8 radius; exine 1 μm thick, reticulate, reticulum developed distally, extending to the proximal pole, brochi \pm uniform in shape, 8–9 in number across in amb view, muri straight or curved, 1.5–3.0 μm high and <1 μm thick, thickness irregular, lumina 4–6 μm across; 31.9–38.8 (35.8 \pm 1.8) \times 20.4–27.2 μm (J. H. Langenheim, Kenai Peninsula, Alaska, 1956, UW 174352), 31.8–38.6 (34.6 \pm 1.7) \times 20.3–24.9 μm (J. A. Calder and L. G. Billard, Moosehide Mountain, Yukon, 1949, UW 176204), 29.5–36.3 (33.6 \pm 1.6) \times 18.2–25.0 μm (J. W. Thompson, Snoqualmie Pass, Washington, 1932, UW). DISTRIBUTION: Kenai Peninsula, Alaska, southeastern Alaska, British Columbia, and northern Washington.

Lycopodium inundatum L.

Monad, radiosymmetric, heteropolar, tetrahedral–sub-spherical; amb circular–subtriangular; trilete, laesurae thin and straight, bordered by an unornamented margo reaching 9 μm across, 0.6–0.8 radius; exine 3–5 μm in thickness, rugulate, becoming verrucate on the proximal face; 35.5–46.6 (41.0 \pm 1.9) \times 20.4–29.5 μm (J. B. Flett, Spanaway, Washington, 1902, UW 42928), 36.2–45.5 (40.4 \pm 1.9) \times 25.0–29.5 μm (H. Murray, Kootenay Lake, British Columbia, 1956, UW 196993), 40.9–52.3 (46.0 \pm 2.5) \times 24.9–36.3 μm (E. F. Layser, Nordman, Montana, 1970, UW 253298). DISTRIBUTION: Southeastern Alaska to northern California.

Lycopodium obscurum L.

Figs. 13, 14, 43, 44
Monad, radiosymmetric, heteropolar, tetrahedral–sub-spherical; amb circular–subtriangular; trilete, laesurae thin and straight, 0.5–0.8 radius; exine <1–1.5 μm thick, reticulate, reticulum almost entirely distal, becoming faint and dissolving beyond the equator, leaving much of the proximal surface unornamented, brochi variable in number and outline, numbering 9–11 across in amb view, frequently incomplete and forming an open network over extensive areas resembling a maze, muri 1–1.5 μm high and 0.5 μm thick, uniform in thickness, straight and curved, lumina reaching 18 μm or more in length, often penetrated by muri branches: 27.1–38.5 (32.6 \pm 2.0) \times 15.9–22.8 μm (O. D. Clark, Nushagak, Alaska, 1938, UW 45749), 27.2–38.7 (33.1 \pm 2.2) \times 18.3–25.0 μm (W. J. Eyerdam, Annette Island, Alaska, 1947, UW 118056), 29.5–36.6 (32.8 \pm 1.9) \times 18.2–22.9 μm (J. A. Calder, D. B. O. Savile, and J. M. Ferguson, Ft. McLeod, Alaska, 1954, UW 174329). DISTRIBUTION: Southeastern Alaska to northern Washington; Attu Island, westernmost of the Aleutian Islands.

Lycopodium selago L.

Figs. 15, 16, 45, 46
Monad, radiosymmetric, heteropolar, tetrahedral–sub-spherical; amb triangular with concave sides and blunt to rounded apices or amb subcircular; trilete, laesurae narrow and straight, extending to the equator; exine 1–4 μm thick; foveolate, fovea \pm uniformly distributed, 1–3 μm apart, most prominent on the distal face; 29.7–40.8 (35.3 \pm 2.3) \times 20.4–29.4 μm (E. H. and H. B. Looff, Kodiak Island, Alaska, 1938, UW 46054), 34.4–45.7 (38.8 \pm 1.7) \times 22.1–28.9 μm (D. M. Peteet, Yakutat, Alaska, 1982, NYU), 35.7–49.5 (41.9 \pm 2.6) \times 20.0–28.9 μm (C. J. Heusser, above Terentiev Lake, west of Columbia Glacier, Prince William Sound, Alaska, 1978, NYU). DISTRIBUTION: Aleutian Islands, Alaska, to southern Washington. Note: Spores described are gradational with what appear to be aberrant forms, perhaps nonfunctional, including subspherical specimens that are foveolate–fossulate, becoming rugulate, exhibit no distinct tetrad scars, and measure approximately 40–49 μm .

Lycopodium sitchense Ruprecht

Figs. 17, 18, 47, 48
Monad, radiosymmetric, heteropolar, tetrahedral–sub-spherical; amb circular–subtriangular; trilete, laesurae thin, straight, 0.6–0.8 radius; exine 1 μm or less thick, reticulate, reticulum on proximal and distal faces, breaking up outside the proximal polar area, brochi variable, 7–8 in number across in amb view, muri straight or somewhat curved, <1 μm thick, irregular in thickness, height increasing from 2 at the distal pole to 3.5 μm at the equator, lumina mostly 6–7 μm across, elongate lumina >10–18 μm in length, penetrated by muri branches; 34.0–45.4 (39.5 \pm 1.9) \times 22.8–29.7 μm (J. W. Thompson, Guy Peak, Washington, 1936, UW), 31.8–45.3 (38.9 \pm 2.8) \times 20.4–29.5 μm (J. A. Calder and K. T. MacKay, Vancouver Island, British Columbia, 1961, UW 233411), 34.1–43.1 (37.5 \pm 2.1) \times 22.7–29.6 μm (J. W. Thompson, Snoqualmie Pass, Washington, 1932, UW). DISTRIBUTION: Aleutian Islands, Alaska; south-central Alaska to northern Oregon.

Key

1. Reticulate.....
2. Reticulum and (or) sculpture elements distinctly developed on proximal faces.....

3. Reticulum breaking up into muri fragments in the proximal polar area	<i>Lycopodium clavatum</i>
3. Reticulum extending as muri branches toward the proximal pole	4
4. Brochi pattern typically discontinuous on distal faces	<i>Lycopodium alpinum</i>
4. Brochi pattern distally \pm uniform	5
5. Muri thickness variable	<i>Lycopodium complanatum</i>
5. Muri thickness \pm uniform	<i>Lycopodium sitchense</i>
2. Reticulum absent or poorly developed proximally	3
3. Brochi number 6–8 across in amb view, muri as much as 3 μm in height at the equator	<i>Lycopodium annotinum</i>
3. Brochi 9–11 across in amb view, frequently incomplete, distally forming open networks over large areas, muri reaching 1.5 μm in height	<i>Lycopodium obscurum</i>
1. Foveolate or rugulate	2
2. Foveolate, amb triangular with concave sides and blunt or rounded apices or amb subcircular, laesurae without margo	<i>Lycopodium selago</i>
2. Rugulate on the distal face, amb circular–subtriangular, laesurae bordered by a broad margo	<i>Lycopodium inundatum</i>

Selaginella

Selaginella densa Rydb. Figs. 19, 20, 49, 50
Monad, radiosymmetric, heteropolar, tetrahedral–sub-spherical; amb circular–subtriangular, irregular in outline; trilete, laesurae narrow, generally straight, somewhat ridged, 0.5–0.8 radius; perine <1 μm thick, psilate, variously cristate, cristae mostly distal, spore 0.7–0.9 radius of the perine envelope; 33.0–53.2 (44.0 \pm 2.8) \times 22.2–31.0 μm (K. H. Lackschewitz, Bitterroot Mountains, Missoula County, Montana, 1971, NY 2856), 37.7–55.4 (46.2 \pm 2.4) \times 26.4–39.6 μm (W. R. Buck, Larimer County, Colorado, 1984, NY 11724), 39.6–55.0 (47.0 \pm 2.2) \times 30.8–37.4 μm (R. M. Tryon, Jr., Colorado Mountains, Colorado, 1952, NY). DISTRIBUTION: Southeastern Alaska to northern California.

Selaginella douglasii (Hook. & Grev.) Spring Figs. 21, 22, 51, 52
Monad, radiosymmetric, heteropolar, tetrahedral; amb subtriangular; trilete, laesurae straight or irregular, reaching the equator, marked by ridges of continuous or broken thickenings; exine 1–5 μm thick, dense, fossulate on the distal side, deeply dissected by fossulae; 28.8–39.9 (34.9 \pm 1.3) \times 22.2–26.6 μm (C. G. Pringle, Cascade Mountains, Oregon, 1881, NY), 28.6–41.8 (36.5 \pm 1.7) \times 22.0–28.6 μm (H. M. Gilkey, Multnomah County, Oregon, 1959, NY 7496), 28.9–44.4 (39.4 \pm 2.3) \times 22.0–30.8 μm (M. Ownbey and G. H. Ward, Selway River, Idaho County, Idaho, 1947, UW 132717). DISTRIBUTION: Southwestern Washington and northwestern Oregon.

Selaginella oregana D. C. Eaton Figs. 23, 24, 53, 54
Monad, radiosymmetric, heteropolar, tetrahedral–spherical; amb circular–subtriangular, irregular in outline; trilete, laesurae with variably thickened ridges, 0.5–0.7 radius; perine 1–1.5 μm thick, coarsely cristate, both distally and proximally, spore 0.7–0.8 radius of the perine envelope; 40.0–60.0 (49.1 \pm 2.9) \times 31.0–37.7 μm (T. D. Trana, Olympic National Park, Washington, 1978, NY 5621), 48.8–64.4 (55.6 \pm 2.7) \times 28.9–40.9 μm (A. N. Steward, Beaver Creek, Oregon, 1954, UW 186354), 48.8–66.6 (56.5 \pm 1.0) \times 33.3–40.0 μm (C. G. Pringle, Coos River, Oregon, 1881, NY). DISTRIBUTION: Western Washington to northwestern California.

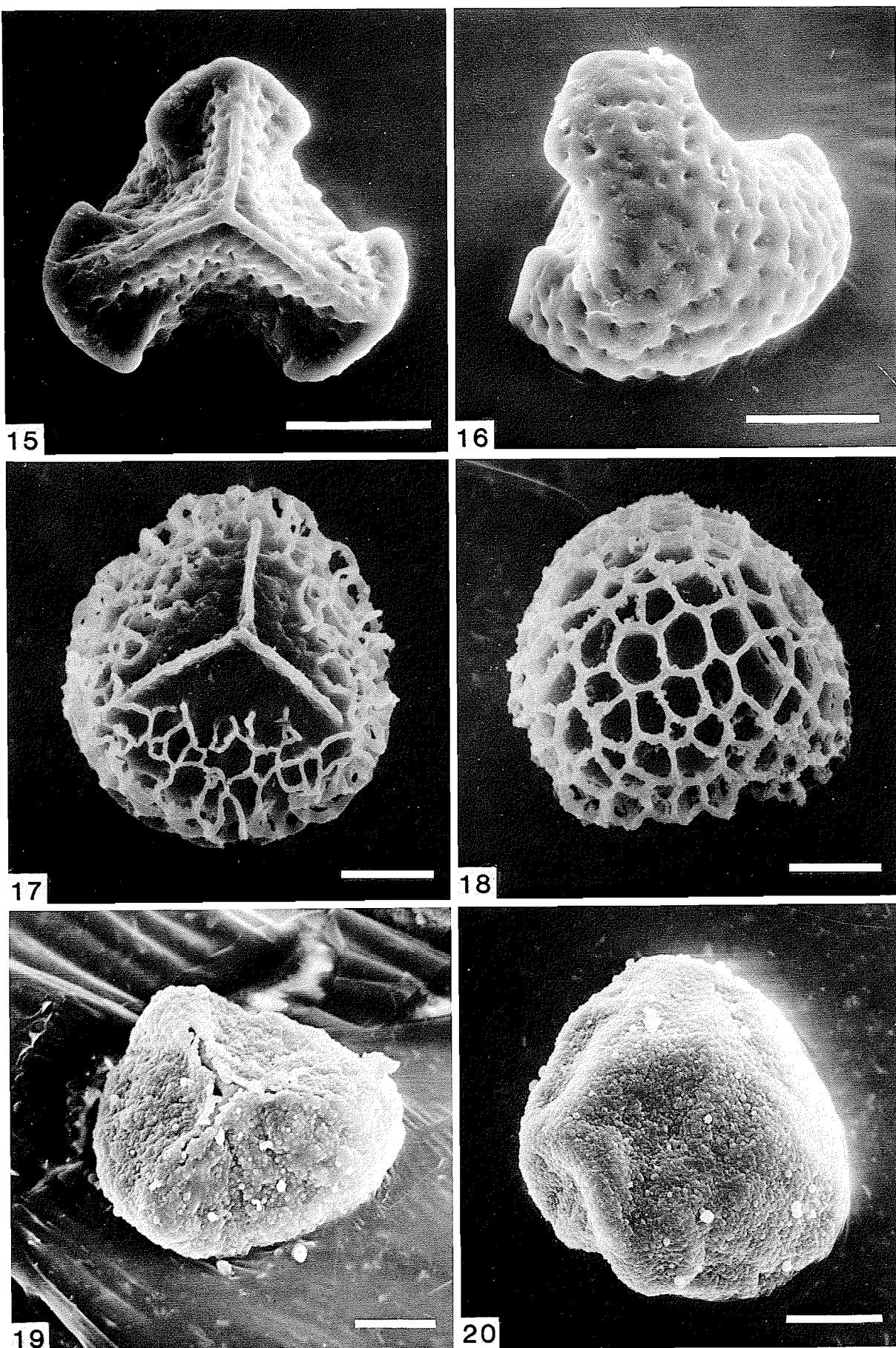
Selaginella selaginoides (L.) Link Figs. 25, 26, 55, 56
Monad, radiosymmetric, heteropolar, tetrahedral–sub-spherical, frequently tetrahedral and hexahedral tetrad; amb

subtriangular; trilete, laesurae straight, narrow, 0.8–0.9 radius; exine 1–2 μm thick, echinate distally, echini straight or curved, pointed, cleft, or blunt at their tips, as much as 10 μm in length, rising from broad bases; 37.7–55.5 (43.3 \pm 2.4) \times 31.0–37.7 μm (J. Thieret and R. Reich, Mackenzie River Highway, Northwest Territories, 1959, NY 5217), 39.9–55.5 (47.2 \pm 2.1) \times 33.3–40.0 μm (J. Taylor and C. Taylor, south of Delta Junction on Delta River, Alaska, 1975, NY 19783), 42.2–62.2 (53.7 \pm 2.5) \times 37.7–42.2 μm (T. M. Taylor, A. F. Szczawinski, and M. Bell, Mile 46, Haines Road, British Columbia, n.d., UW 182073). DISTRIBUTION: Aleutian Islands, Alaska, to southern British Columbia.

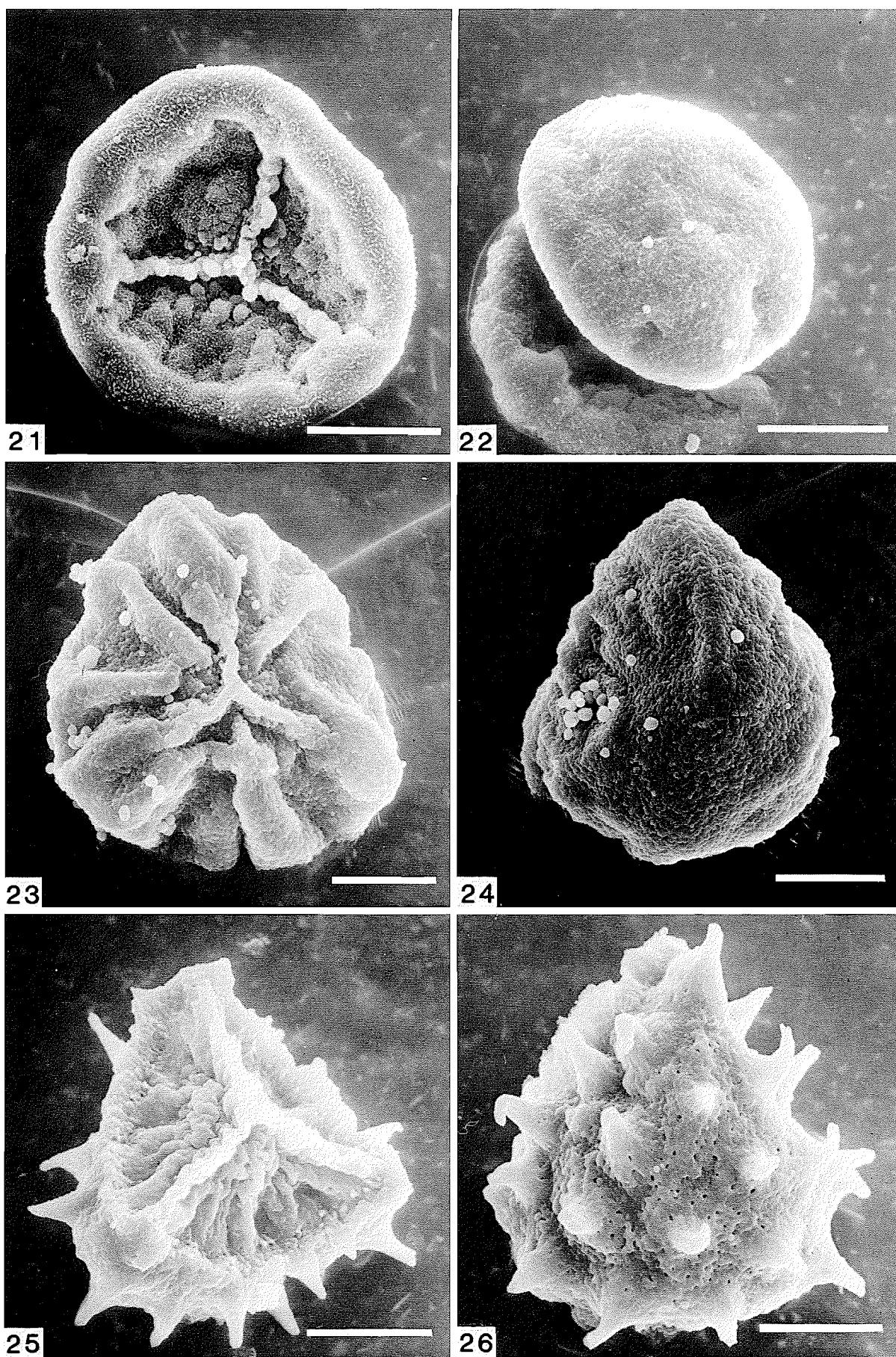
Selaginella sibirica (Milde) Hieron. Figs. 27, 28, 57, 58
Monad, radiosymmetric, heteropolar, tetrahedral–sub-spherical; amb subtriangular–subcircular, irregular in outline; trilete, laesurae straight, narrow, 0.5–0.8 radius; perine 1.5–2 μm thick, psilate, cristae on distal and proximal faces moderately developed, microsculpture on proximal faces relatively coarse, spore 0.8–0.9 radius of the perine envelope; 35.5–55.5 (44.2 \pm 2.8) \times 26.6–31.1 μm (G. L. Smith, Utukok River, northern Alaska, 1966, NY 2957), 37.7–55.4 (46.7 \pm 2.4) \times 33.3–37.6 μm (J. B. Flett, west of Nome, Alaska, 1900, NY 1532), 40.0–55.5 (47.0 \pm 2.1) \times 26.6–37.7 μm (A. E. Porsild and R. T. Porsild, Mackenzie River Delta, Northwest Territories, 1927, NY 2031). DISTRIBUTION: Unalaska Island, Aleutian Islands, and Kenai Peninsula, Alaska.

Selaginella wallacei Hieron. Figs. 29, 30, 59, 60
Monad, radiosymmetric, heteropolar, tetrahedral–sub-spherical; amb subtriangular; trilete, laesurae straight, narrow, often appearing ridged, 0.5–0.8 radius; perine <1 μm thick, psilate, spore 0.6–0.9 radius of the perine envelope; 31.1–48.8 (39.8 \pm 2.9) \times 19.6–30.2 μm (A. W. Kruckeberg, vicinity of Lake Cle Elum, Washington, 1960, UW 218814), 37.7–51.1 (43.4 \pm 1.6) \times 24.4–33.3 μm (W. H. Baker, Craig Mountains, Nez Perce County, Idaho, 1950, NY 6516), 40.0–53.3 (46.8 \pm 1.7) \times 24.4–31.1 μm (R. Kaul and D. Sutherland, near Selway River, Idaho County, Idaho, 1971, NY 3064). DISTRIBUTION: Southern British Columbia to northern California.

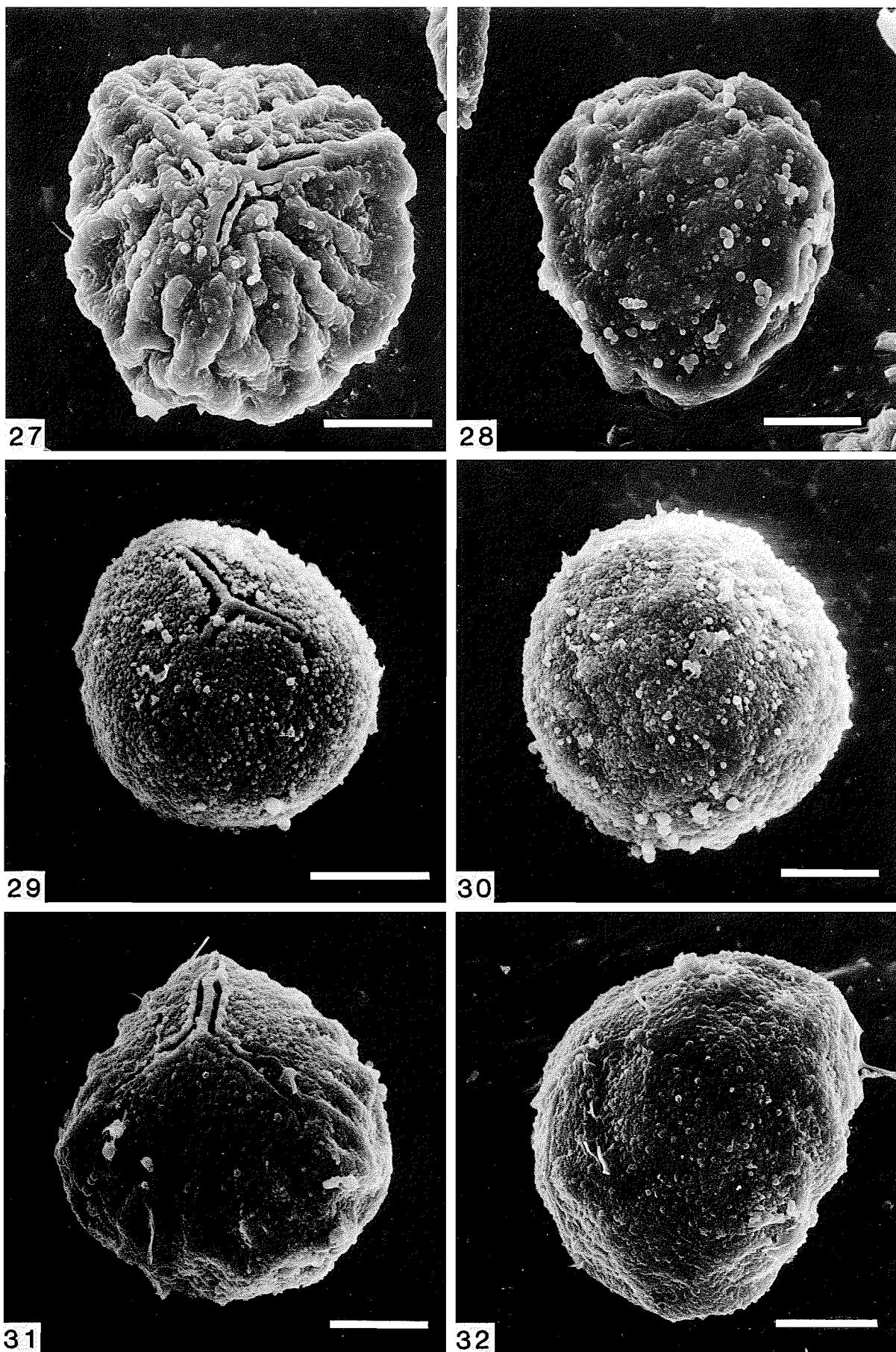
Selaginella watsonii Underw. Figs. 31, 32, 61, 62
Monad, radiosymmetric, heteropolar, tetrahedral–spherical; amb circular–subtriangular; trilete, laesurae straight, narrow, 0.6–0.8 radius; perine 2–3 μm thick, psilate, cristae



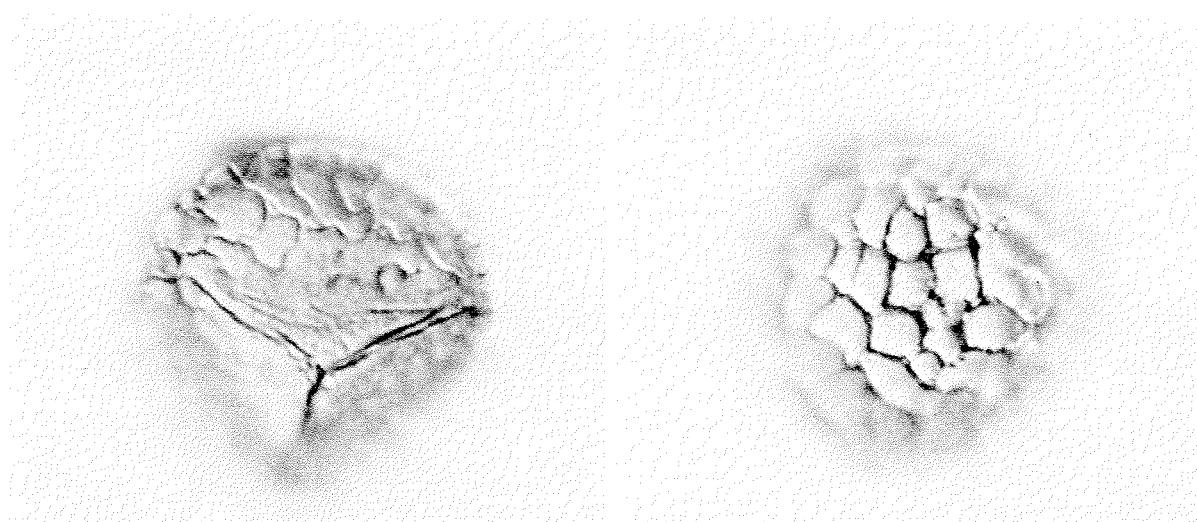
Figs. 15-20. Spore scanning electron micrographs of *Lycopodium selago*, proximal view (Fig. 15), distal view (Fig. 16); *L. sitchense*, proximal view (Fig. 17), distal view (Fig. 18); *Selaginella densa*, proximal view (Fig. 19), distal view (Fig. 20). Scale bar = 10 μm .



Figs. 21–26. Spore scanning electron micrographs of *Selaginella douglasii*, proximal view (Fig. 21), distal view (Fig. 22); *S. oregana*, proximal view (Fig. 23), distal view (Fig. 24); *S. selaginoides*, proximal view (Fig. 25), distal view (Fig. 26). Scale bar = 10 μm .

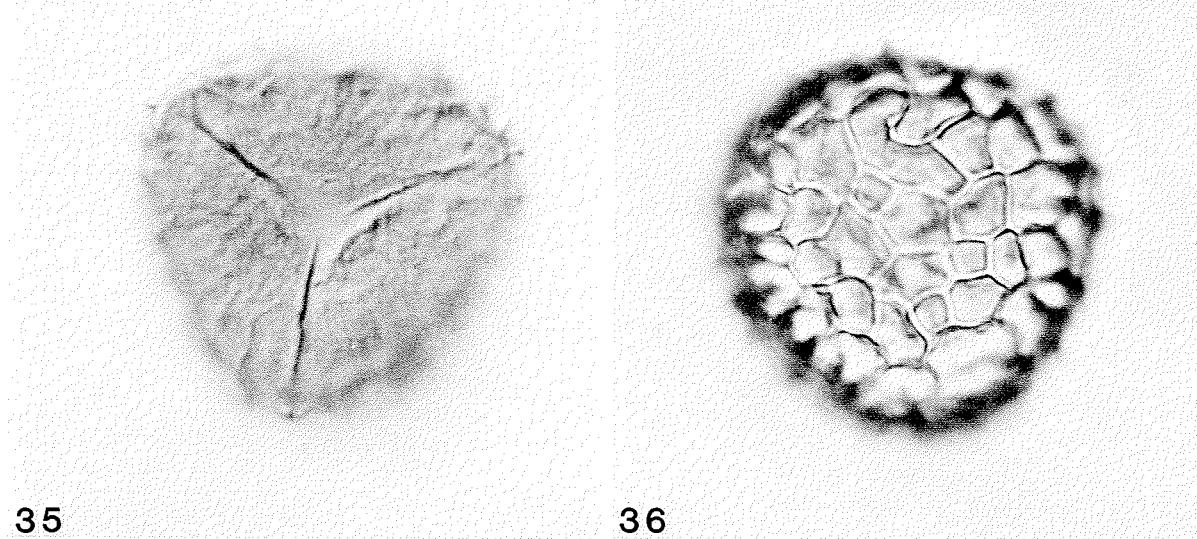


Figs. 27–32. Spore scanning electron micrographs of *Selaginella sibirica*, proximal view (Fig. 27), distal view (Fig. 28); *S. wallacei*, proximal view (Fig. 29), distal view (Fig. 30); *S. watsonii*, proximal view (Fig. 31), distal view (Fig. 32). Scale bar = 10 μm .



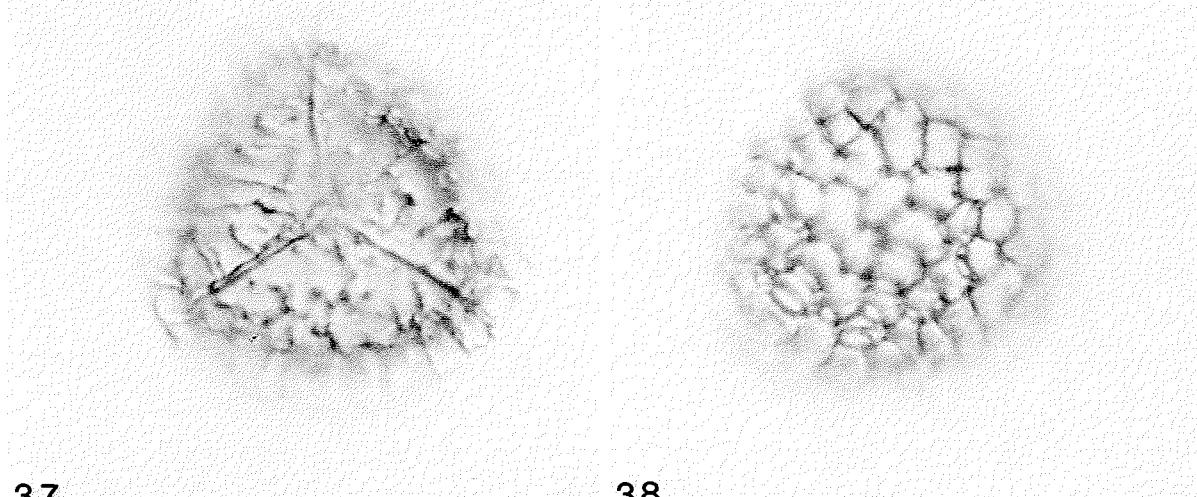
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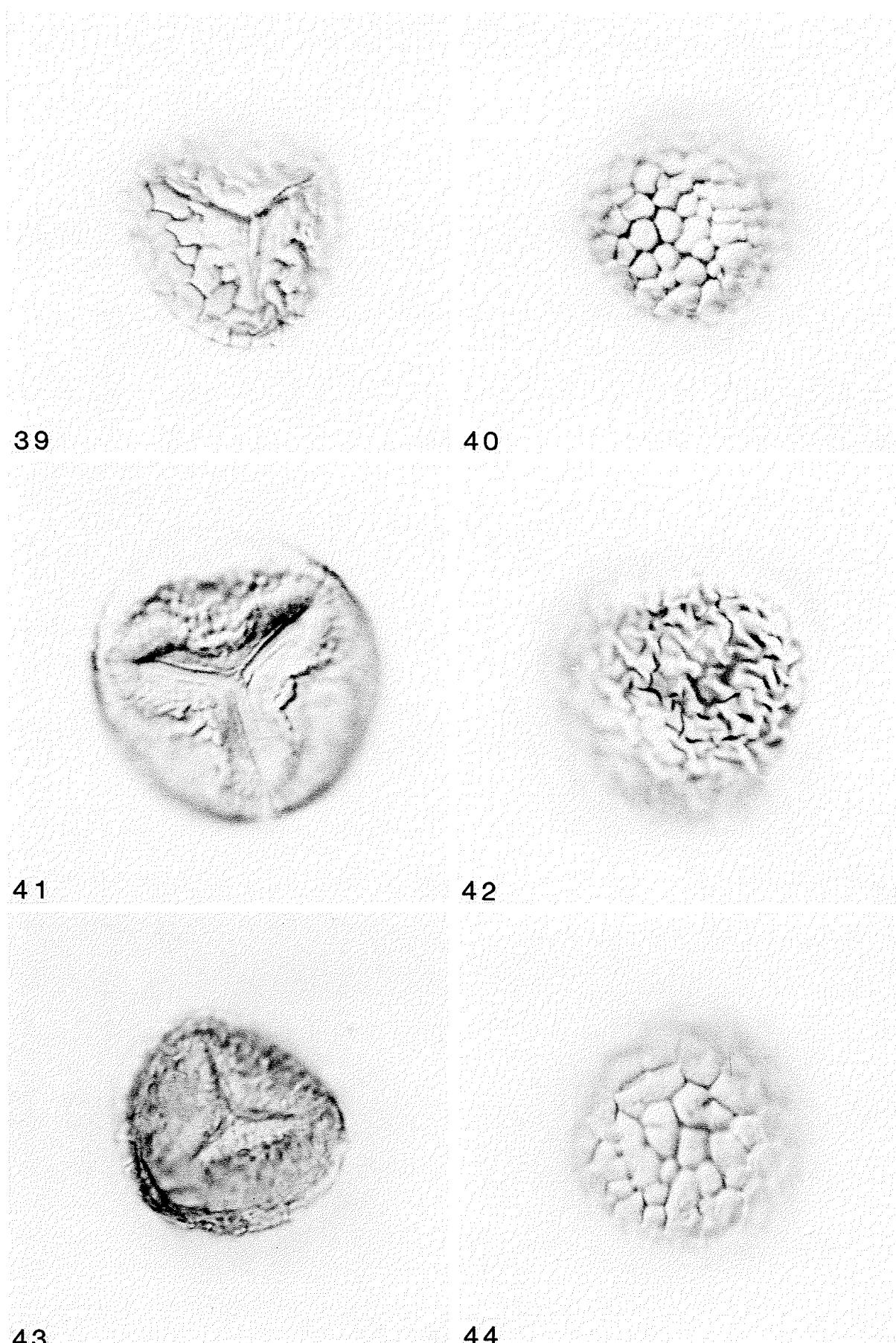
36



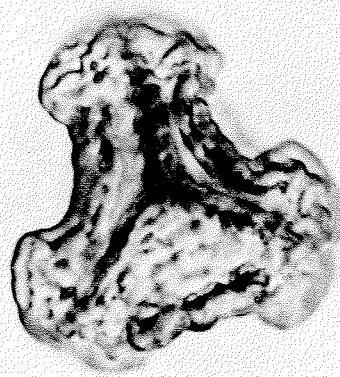
37

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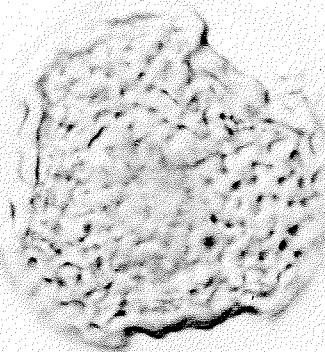
FIGS. 33-38. Spore light micrographs ($\times 1200$) of *Lycopodium alpinum*, proximal view (Fig. 33), distal view (Fig. 34); *L. annotinum*, proximal view (Fig. 35), distal view (Fig. 36); *L. clavatum*, proximal view (Fig. 37), distal view (Fig. 38).



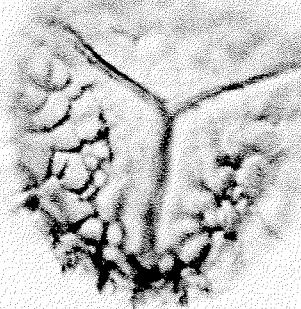
Figs. 39–44. Spore light micrographs ($\times 1200$) of *Lycopodium complanatum*, proximal view (Fig. 39), distal view (Fig. 40); *L. inundatum*, proximal view (Fig. 41), distal view (Fig. 42); *L. obscurum*, proximal view (Fig. 43), distal view (Fig. 44).



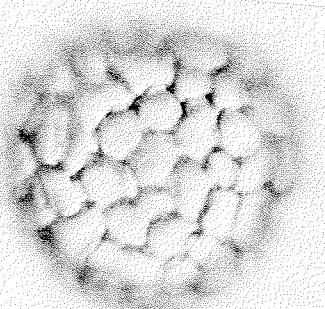
45



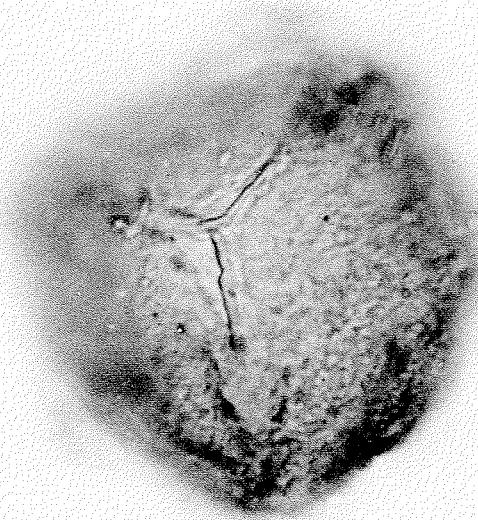
46



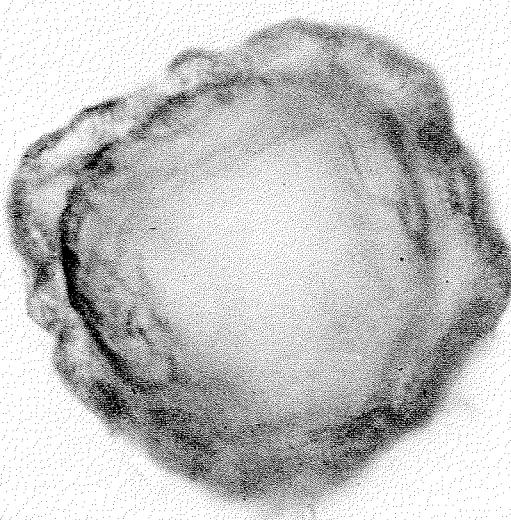
47



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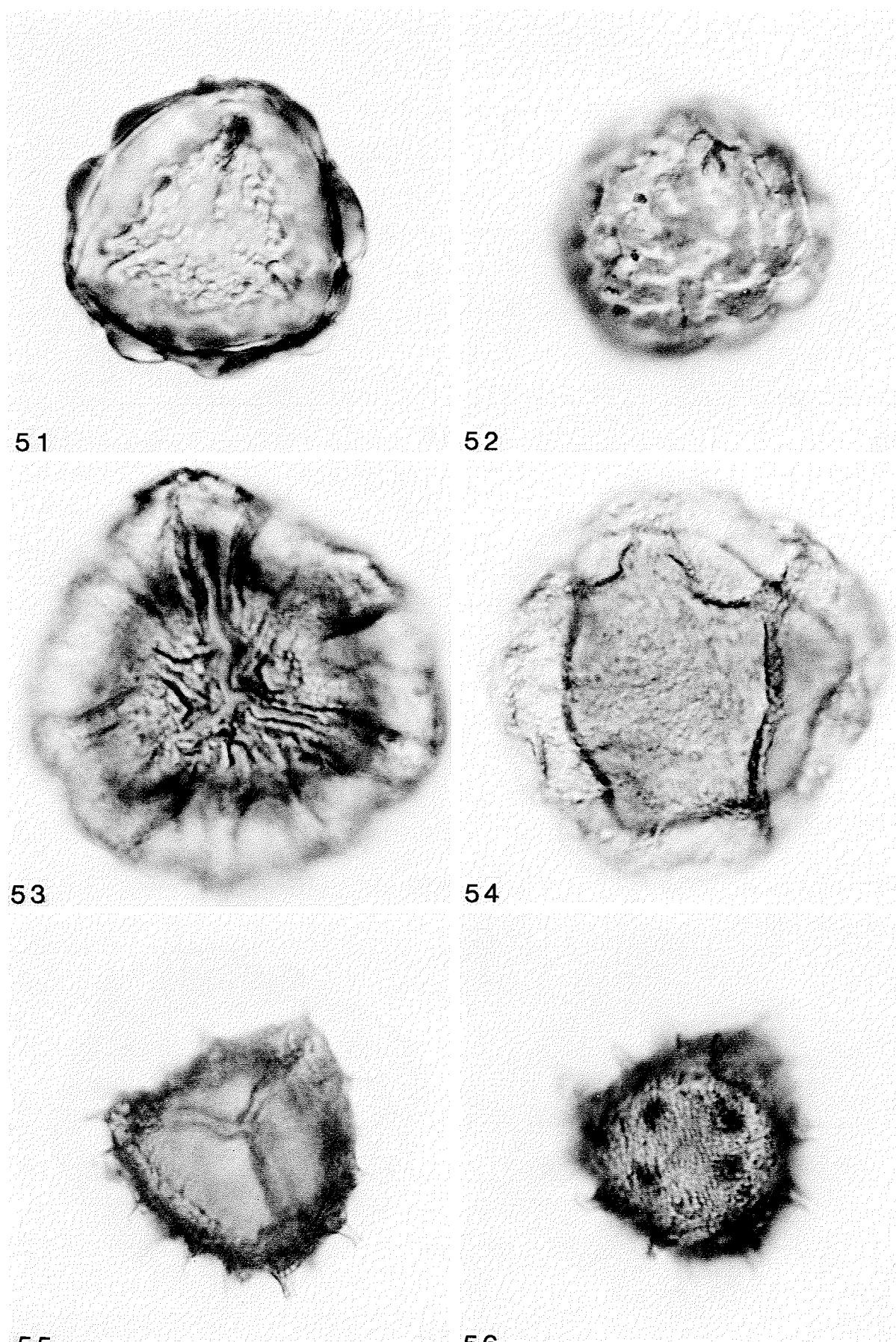


49

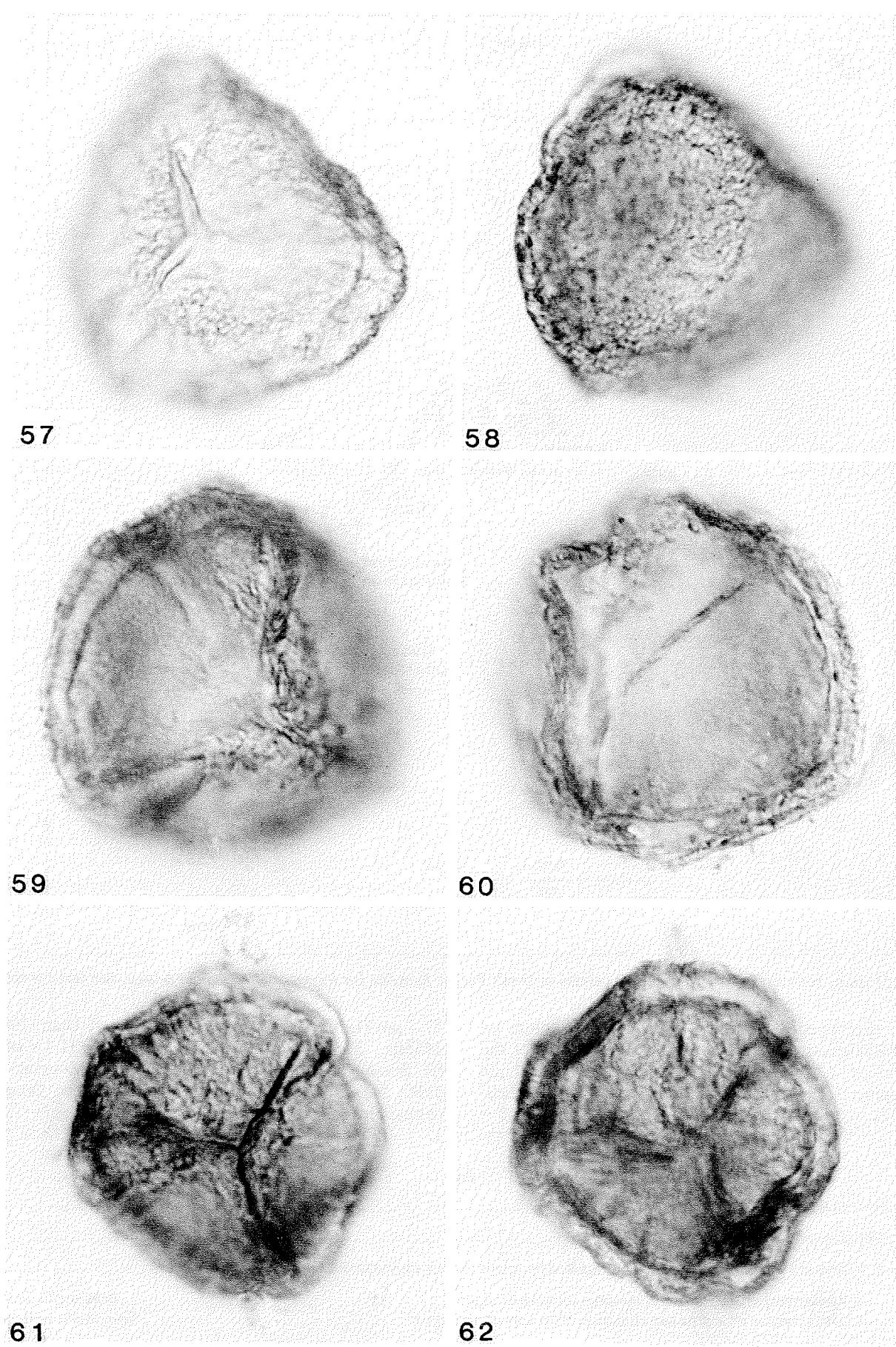


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Figs. 45–50. Spore light micrographs ($\times 1200$) of *Lycopodium selago*, proximal view (Fig. 45), distal view (Fig. 46); *L. sitchense*, proximal view (Fig. 47), distal view (Fig. 48); *Selaginella densa*, proximal view (Fig. 49), distal view (Fig. 50).



Figs. 51–56. Spore light micrographs ($\times 1200$) of *Selaginella douglasii*, proximal view (Fig. 51), distal view (Fig. 52); *S. oregana*, proximal view (Fig. 53), distal view (Fig. 54); *S. selaginoides*, proximal view (Fig. 55), distal view (Fig. 56).



FIGS. 57–62. Spore light micrographs ($\times 1200$) of *Selaginella sibirica*, proximal view (Fig. 57), distal view (Fig. 58); *S. wallacei*, proximal view (Fig. 59), distal view (Fig. 60); *S. watsonii*, proximal view (Fig. 61), distal view (Fig. 62).

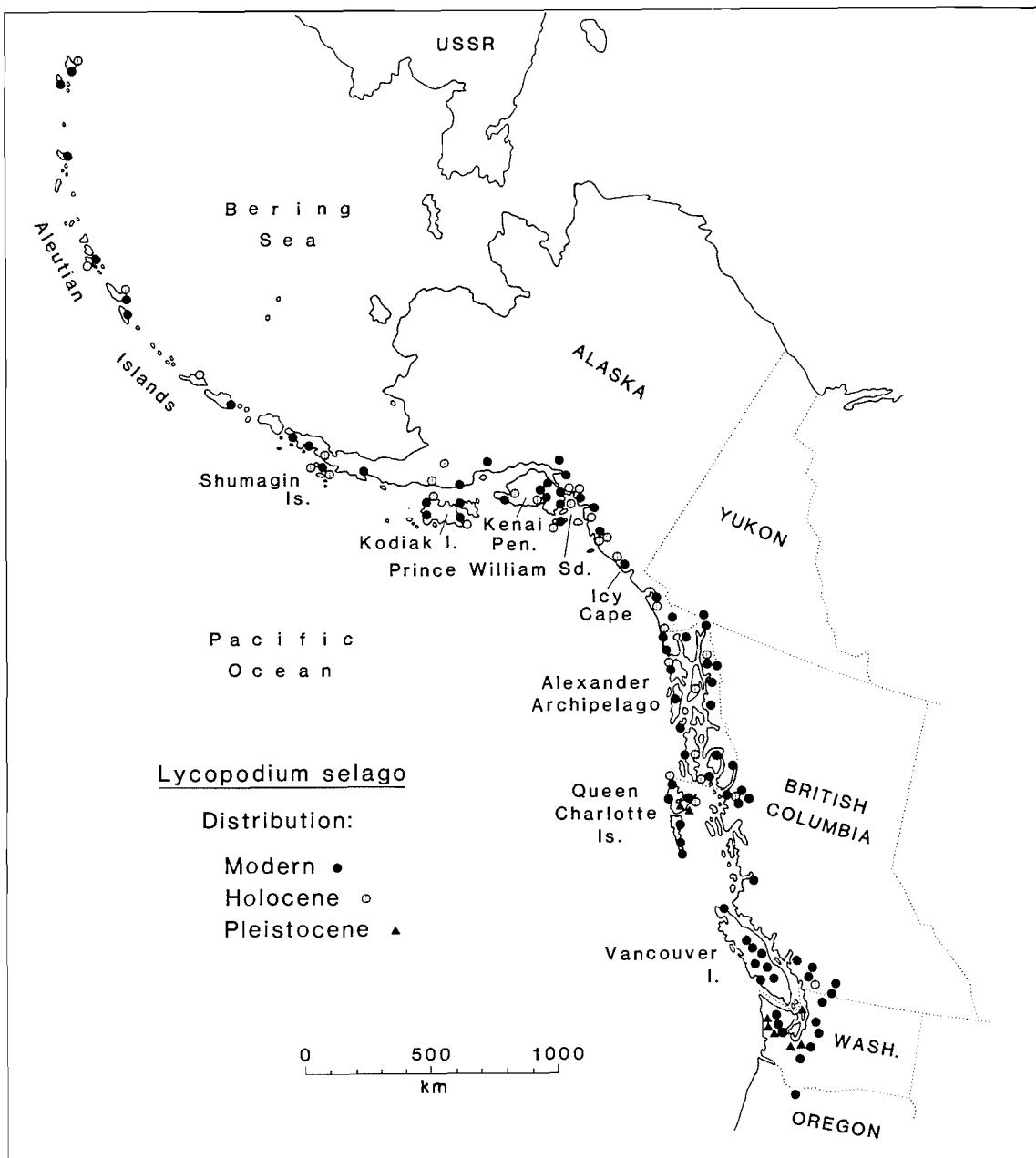


FIG. 63. Modern, Holocene, and Pleistocene localities in North Pacific America for spores of *Lycopodium selago*. See text for sources.

moderately developed and mostly distal, microsculpture on proximal faces relatively fine, spore 0.7–0.9 radius of the perine envelope; $40.0–57.7 (47.3 \pm 2.5) \times 26.6–31.1 \mu\text{m}$ (I. L. Wiggins, Sonora Pass Road, Tuolumne County, California, 1972, NY 11189), $37.7–62.2 (48.6 \pm 3.8) \times 33.3–$

$37.7 \mu\text{m}$ (L. C. Higgins, Salt Lake County, Utah, 1984, NY 14486), $37.7–62.1 (49.8 \pm 3.4) \times 31.1–44.4 \mu\text{m}$ (R. Soreng and R. Spellenberg, Murdock Mountain, Utah, 1980, NY 1335). DISTRIBUTION: Northeastern Oregon and central and southern California.

Key

1. Spores contained in a perine envelope 2
2. Perine relatively thin, distally $< 2 \mu\text{m}$ 3
3. Perine $< 1 \mu\text{m}$ thick, proximal faces marked by relatively few inconspicuous cristae or not at all 4
4. Moderately cristate distally, laesuræ somewhat ridged *Selaginella densa*
4. Distal cristæ absent or rare, laesuræ often appearing ridged *Selaginella wallacei*
3. Perine thicker, proximal faces prominently marked by cristæ *Selaginella oregana*
2. Perine thicker, distally $2–3 \mu\text{m}$ 3

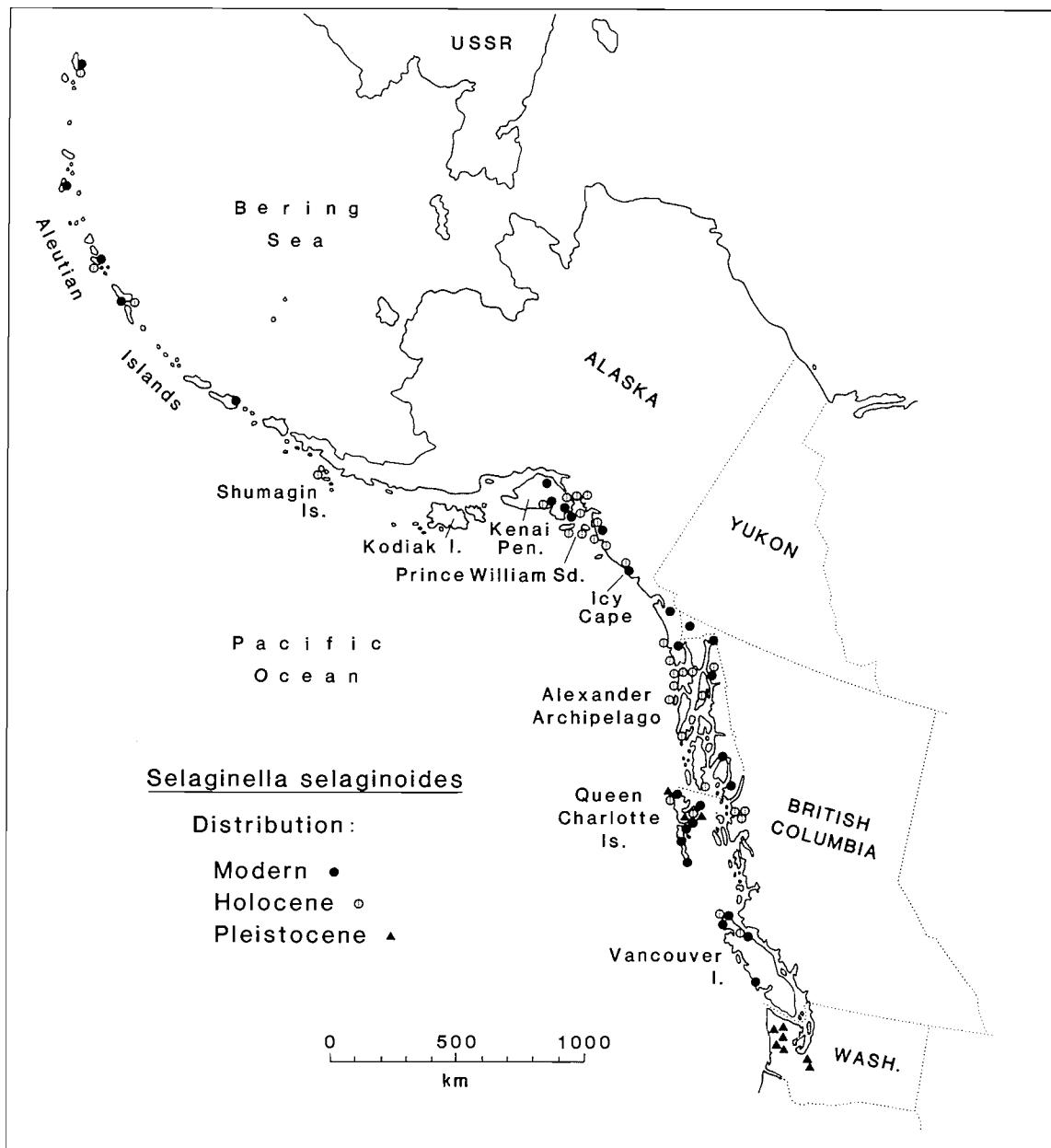


FIG. 64. Modern, Holocene, and Pleistocene localities in North Pacific America for spores of *Selaginella selaginoides*. See text for sources.

- | | |
|---|---------------------------------|
| 3. Proximal microsculpture \pm coarse, species ranging in Alaska..... | <i>Selaginella sibirica</i> |
| 3. Proximal microsculpture finer, species ranging in Oregon and California..... | <i>Selaginella watsonii</i> |
| 1. Perine absent..... | 2 |
| 2. Fossulate, fossulae deeply incised..... | <i>Selaginella douglasii</i> |
| 2. Echinate..... | <i>Selaginella selaginoides</i> |

Quaternary records of *Lycopodium selago* and *Selaginella selaginoides* in North Pacific America

Of all species under consideration, spores of *L. selago* and *S. selaginoides* because of their distinct morphology are most readily identified and frequently observed in regional North Pacific Quaternary deposits. Records are sufficiently substantive to justify presentation of data in a general way on distribution maps (Figs. 63, 64). Data are from sources categorized as modern (Hultén 1941, 1968; Calder and Taylor 1968; Taylor

1970), Holocene (Heusser 1960, 1973, 1978a, 1983a, 1983b, 1983c; C. J. Heusser, unpublished; Mathewes 1973; Warner 1984; Peteet 1986), and Pleistocene (Heusser 1974, 1977, 1978b, 1982, 1983c; C. J. Heusser, unpublished; Heusser and Heusser 1981; Warner 1984; Warner *et al.* 1984).

Modern distribution patterns of *L. selago* and *S. selaginoides* reflect migratory paths from unglaciated Pleistocene refugia located principally in northwestern Washington and the Queen Charlotte Islands, British Columbia (Heusser 1988), and also in the Japanese archipelago — eastern Asia, where

both species grow at present (Ohwi 1984). Spores are contained in interglacial and Wisconsin-age interstadial and glacial, including late-glacial, sediments beyond ice-sheet boundaries. The range difference between Pleistocene and modern distributions implies a climate colder than at present at lower latitudes. In particular, the appearance of *Selaginella selaginoides* in Washington fossil records (Fig. 64) indicates that climatic conditions there were similar to those in coastal Alaska and British Columbia today. Thus, recognition of fossil spores, their present geographic distribution, and past occurrence in sediments are important criteria for reconstructing vegetation and climate.

The paucity of Holocene data in the southern parts of the ranges (Figs. 63, 64) is an indication that surroundings of deposits studied at low altitude have been mostly unsuitable for the two species. For *L. selago*, migration during the Holocene proceeded to higher altitudes locally, as indicated by modern montane or subalpine-alpine collection sites in Washington and southern British Columbia, and to higher latitudes (Fig. 63). For *S. selaginoides*, the southern limit of its range is on western Vancouver Island, and no Holocene or modern sites are known in Washington (Fig. 64).

Northwestward along the coast, modern and Holocene records of *L. selago* (Fig. 63) are regularly distributed, show no major lacunae, and appear conformable. Evidence from the Holocene shows the species close to 10 000 years ago westward in Alaska in the Aleutian Islands, so that it is not possible to ascertain the course of migratory movement from sources on the American continent and (or) from Japan-Asia. *Selaginella selaginoides*, on the other hand, exhibits a considerable gap in modern distribution between the Kenai Peninsula and the Aleutian Islands, thus separating the species in the western Aleutians, which appear only 3000-4000 years ago, from populations in southeastern Alaska, which were established around 10 000 years ago. This bipartite pattern and age difference suggest that the species in the Aleutians is derived from a Japanese or Asiatic source and has been slow to migrate eastward. Palynology of marine sediments in the northwest Pacific Ocean off Japan confirms the presence of *S. selaginoides* in ice-free areas on the nearby coast during Wisconsin glaciation (Heusser and Morley 1985). Further investigation of the North Pacific region is needed to define migration pathways, establish the timing of events, and document climatic constraints.

Acknowledgments

We thank M. F. Denton and J. T. Mickel for permission to sample herbarium sheets at the University of Washington and New York Botanical Garden, respectively; M. Yoder for supervision of the scanning electron microscope work; R. J. Hebda for comments on the manuscript; and I. O'Brien and C. A. Sanctetta for technical assistance.

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